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Female-biased dispersal in the solitarily foraging slender mongoose, *Galerella sanguinea*, in the Kalahari

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Sex-biased dispersal is common in most mammals, but a female bias is less so and exceptionally rare in solitary mammals. Here we present genetic and observational evidence for strong female-biased dispersal in a solitary foraging small carnivore, the slender mongoose. We suggest that females benefit from dispersal by avoiding kin competition over local resources and inbreeding, while males can benefit from philopatry through kin cooperation leading to an increased success in female defence. The comparison between our observations and those of a previous study in Tanzania suggest that there is ecologically influenced flexibility in dispersal patterns within this species, influencing sex-specific benefits of dispersal and philopatry. Comparing our results with those on the closely related, more social mongoose species in which both sexes commonly disperse suggests that dispersal patterns are linked to a species' social system by the opportunity, or lack of it, in philopatry to obtain unrelated mating partners and gain indirect fitness benefits.

Keywords: female-biased dispersal, female inbreeding avoidance, *Galerella sanguinea,* **male philopatry, slender mongoose, solitary mammal**

47 Natal dispersal, the permanent movement of an animal from its natal range or group to the
48 place where it reproduces (Clutton-Brock, 1989; Clutton-Brock & Lukas, 2012; Greenwood,
49 1980; Howard, 1960; Waser, 1996; Waser & Jones, 1983) is one of the most important
50 aspects of its life history (Lawson Handley & Perrin, 2007). It is a shift in range and feeding
51 locations, representing a potentially profound change in environmental conditions (Smale,
52 Nunes, & Holekamp, 1997), and in the genetic dissimilarity to oneself in conspecifics to be
53 encountered. In most species dispersal among offspring differs between the sexes (reviewed
54 in: Greenwood, 1980; Lawson Handley & Perrin, 2007). Sex-biased dispersal results from sex
55 differences in dispersal rate and/or distance (Lawson Handley & Perrin, 2007) and has
56 consequences for the genetic structure of a population (Clobert, Danchin, Dhondt, & Nichols,
57 2001). Numerous studies have investigated the reasons for sex-biased dispersal, the consensus
58 being that it is ultimately based on an interaction of inbreeding avoidance (Clutton-Brock,
59 1989), avoidance of kin competition (local resource competition) between females (Clark,
60 1978; Greenwood, 1980), local mate competition between males (Dobson, 1982; Hamilton,
61 1967; Moore & Ali, 1984) and kin cooperation (Greenwood, 1980, Lawson Handley & Perrin,
62 2007) resulting from the social system of a species. Most mammals show a male bias in
63 dispersal, which has been linked to their predominantly polygynous mating systems, where
64 male local mate competition exceeds female local resource competition (Greenwood, 1980,
65 Lawson Handley & Perrin, 2007).

66 Female-biased dispersal is less common in mammals and provides an interesting opportunity
67 to investigate evolutionary causes of sex-biased dispersal. It is found across phylogenetically
68 diverse taxonomic groups, ranging from chimpanzees, *Pan troglodytes* (Nishida et al., 2003),
69 to greater white-toothed shrews, *Crocidura russula* (Favre, Balloux, Goudet, & Perrin, 1997),
70 and African wild dogs, *Lycaon pictus* (McNutt, 1996) and across all forms of mating systems.
71 Female-biased dispersal has been associated with resource-defence systems in which males
72 actively defend resources and/or a territory to attract females (white-lined bats, *Saccopteryx*

bilineata, Bradbury & Vehrenkamp, 1976; 1977; North American porcupine, *Erethizon dorsatum*, Sweitzer & Berger, 1998) as well as systems in which males benefit from kin cooperation in preventing extragroup males gaining access to their females (Lawson Handley & Perrin, 2007). A dominant view is that female-biased dispersal is linked to inbreeding avoidance, where male tenure is longer than female age at first conception (greater sac-winged bats, *Saccopteryx bilineata*, Nagy, Heckel, Voigt, &Mayer, 2007; hamadryas baboons, *Papio hamadryas*, African wild dogs, Clutton-Brock, 1989; Clutton-Brock & Lukas, 2012).

Solitary species, those that spend most of their lives on their own, have gained less attention in studies of dispersal patterns, even though individuals in solitary species are still part of a network of social interactions with conspecifics that greatly affect their behaviour (Leyhausen, 1965). They should prove especially interesting in answering questions about the influence of social systems as a whole, defined as the combination of a species' social organization, social interactions and mating system (Kappeler & van Schaik, 2002) on dispersal patterns. Studies on solitary carnivores such as bears, *Ursus americanus, Ursus arctos*, tigers, *Panthera tigris*, cougars, *Puma concolor*, and raccoons, *Procyon lotor* (Biek et al., 2006; Moyer, McCown, Eason, & Oli, 2006; Ratneyeke, Tuskan, & Pelton, 2002; Smith, 1993; Støen, Bellemain, Sæbø, & Swenson, 2005) as well as solitary woodrats, *Neotoma fuscipes* (McEachern, Eadie, Van Vuren, 2007) show male-biased dispersal patterns as in most social mammals. A similar pattern has been found in orang-utans, *Pongo pygmaeus* (Arora et al., 2012; Nietlisbach et al., 2012). Female-biased dispersal in solitary mammals is very rare. To our knowledge only two solitary species with a female bias in dispersal have been described so far (see also Lawson Handley & Perrin, 2007): the common wombat, *Vombatus ursinus* (Banks, Skerratt, & Taylor, 2002) and the kinkajou, *Potos flavus* (Kays, Gittleman, & Wayne, 2000). Both species have a polygynous to promiscuous mating system

98 and show resource defence in which philopatric, related males seem to cooperate to defend a
99 common resource and attract females (Kays et al., 2000, Banks et al., 2002).

100 Here we investigated the dispersal behaviour of the Kalahari slender mongoose. The slender
101 mongoose is a small (400–700 g), solitarily foraging, diurnal mongoose species, ranging
102 throughout Africa south of the Sahara with the possible exception of dense rain forests
103 (Taylor, 1975). It is an opportunistic carnivore feeding on small vertebrates (birds, reptiles,
104 small rodents) but also a wide array of invertebrates (Rood & Waser, 1978; Taylor, 1975; B.
105 Graw, M. B. Manser, personal observation) and carrion (Vaughan, 1976). The slender
106 mongoose has been described as solitary (Maddock & Perrin, 1993; Rood, 1989) but detailed
107 information on its social system is lacking. We looked specifically at sex differences in
108 dispersal and compared our results with those from another population studied in East Africa
109 (Rood & Waser, 1978; Waser, Keane, Creel, Elliott, & Minchella, 1994) and two sympatric
110 mongoose species, the meerkat, *Suricata suricatta*, and yellow mongoose, *Cynictis*
111 *penicillata*. We used a combination of genetic and behavioural data to address who disperses
112 and how far. In this paper we discuss our results in the light of information that has become
113 recently available through other aspects of our long-term study on the slender mongoose in
114 the Kalahari.

115

116 **<H1>Methods**

117 *<H2>Study population*

118 We studied slender mongooses in the southern Kalahari at the Kuruman River Reserve
119 (26°58'S; 21°49'E), South Africa, where it occurs sympatrically with the obligate social
120 meerkat, and the facultatively social yellow mongoose. In this population, slender mongooses
121 forage almost exclusively solitarily, with the exception of mothers and their dependent

offspring. They live in spatial groups consisting of one to three adult males that greatly overlap in their home ranges and overlap the ranges of one to four females (Graw & Manser, 2015b). Female ranges are smaller and more exclusive (Graw & Manser, 2015b). Within spatial groups mongooses show communal denning between adult males and between adult males and a female. Females never den communally with other adult females and there is no communal denning between animals of different spatial groups (Graw & Manser, 2015b). Slender mongooses in the Kalahari breed during the wet summer months (October–March) and females give birth to one to three pups per litter and one or two litters per season. Females raise their offspring without the assistance of males. Pups are born in hollow trees in which they remain until emergence, followed by a period of foraging alongside mothers until independence around 4 months of age (Graw & Manser, 2015a).

<H2>Sampling

Animals were captured throughout the study area between June and December 2007 and between May 2008 and May 2011 using box traps (Standard Humane Cage Trap, Animal Handling Support Systems, Johannesburg, South Africa). Traps were prebaited with raw mincemeat, egg and small bones for 3 days prior to capture, followed by 3 days of capturing. Most captures were done in six focal areas, in which animals were fitted with VHF radiocollars (Sirtrack, Havelock North, New Zealand; Biotrack, Wareham, U.K.) and targeted specific animals using traps located at their sleeping sites or in locations often frequented by that animal. To sample as much of the population as possible, capture efforts were increased during winter months (May–September), when slender mongooses were hungry and more likely to enter traps. Winter captures included areas not frequented by our main focal animals, longer capture sequences (5–7 days) and more traps/area (average distance between traps: 300 m).

All captured mongooses were permanently marked with a subcutaneous microchip (Identipet, Muldersdrift, South Africa), sexed, measured and aged according to weight and tooth wear (Graw & Manser 2015a) before a small tissue sample (2–3 mm) of the tail tip was taken. Samples were stored in 90% ethanol and frozen. During 215 captures, 131 individuals belonging to nine different spatial groups (Graw & Manser, 2015b) were sampled and identified.

<H2>Observational and tracking data

We recorded all incidences of dispersal and philopatry during our study period. This was based on observations of marked individuals, tracking of radiocollared animals and recapture events of dispersers. We considered an animal as having dispersed if we recaptured it as an adult in a location that was not the range in which it was born. To exclude potential cases of extraterritorial prospecting followed by an animal returning to its natal range we controlled for the distance between capture locations and checked the locations of consecutive observations and captures of the individual.

<H2>Ethical note

The study was conducted under the permission of the ethical committee of Pretoria University and the Northern Cape Conservation Service, South Africa (Permit number: EC054-10).

Capture methods followed standard procedures previously employed for the capture of yellow mongooses (le Roux 2007). Slender mongooses were caught using box traps (Standard Humane Cage Trap, Animal Handling Support Systems) covered in shade net to minimize

visibility of approaching researchers and reduce heat stress. On capture days, traps were checked every 20–60 min. Captured mongooses were immediately transferred to cloth bags to reduce handling time and simplify injections. Individuals were anaesthetized using an intramuscular injection of 2 – 6 mg/kg Zoletil (Tiletamin – Zolazepam, Virbac, Switzerland). Induction time was on average 2 min. Morphological measurements, placing of microchips, DNA sampling and collaring were all done while animals were fully anaesthetized. After procedures animals were placed in an aerated recovery box and placed in the shade. Mongooses were closely monitored until full recovery and released at the capture site 45 - 90 min after capture. We observed no negative aftereffects to the drug, nor did animals become trap-shy.

Only adults weighing at least 440 g (females) or more than 570 g (males) were collared. Radiocollars, single-stage (Sirtrack) or two-stage (Biotrack) VHF transmitters, weighed 14 - 18 g, equivalent to not more than 4% of a mongoose's body weight. Collars were fitted to allow weight gain but not slip or enable the animal to get a paw stuck under it, by measuring tightness with the tip of a small finger. Screws and bolts were additionally prevented from loosening by sealing them with superglue and each collar was marked by colour-coded shrink-wrap fitted over the bolt. Individuals were caught up to five times during the study period, and generally not more than twice a year, except in cases where a broken collar needed to be replaced. The longest-tracked individual was followed for 29 months. All collars were removed at the end of the study.

<h2>Microsatellite genotyping

From a single skin sample 5–10 µg of DNA was extracted using a salt extraction method (Müllenbach, Lagoda, & Welter, 1989). Individuals were genotyped using 10 microsatellite

markers (Appendix, Table A1) gained through cross-species amplification (see Appendix). PCR reactions were conducted in two multiplex sets with the Qiagen multiplex PCR Kit (www.quiagen.com) using 20–50 ng of DNA, 0.025–0.4 µM of each primer and the following cycle regime: an activation step at 94 °C for 15 min followed by 35 cycles of 30 s denaturation at 94 °C, annealing for 90 s at 57 °C and extension for 120 s at 72 °C, followed by a final extension at 72 °C for 20 min. Allele sizes were analysed after capillary gel electrophoresis in an ABI 3730 DNA-Analyzer using GeneMapper 4.0 (Applied Biosystems, Foster City, CA, U.S.A.).

<H2>Genetic analysis

Error rates per locus were calculated manually from the proportion of mismatched genotypes of 61 samples that were genotyped twice (47% of all samples). Tests for Hardy–Weinberg equilibrium were conducted with GenePop 4.1.3 (Rousset, 2008; Raymond & Rousset, 1995) using only adult individuals to avoid overlapping generations. With Micro-Checker 2.2.3 (Van Osterhout, Hutchinson, Wills, & Shipley, 2004) we tested for the presence of null alleles.

Error rate per allele over all 10 loci was 0.005 (range 0–0.0333) but was entirely based on two loci. Ssu13.8 had a per allele error rate of 0.0333 and Ssu7.1 one of 0.0172; the others showed no errors. Tests for Hardy–Weinberg equilibrium revealed one locus (Hj34) deviated from HW equilibrium (Appendix, Table A1), which was excluded from further analyses. Micro-Checker found one locus (Ssu13.9) to potentially have null alleles. It was removed from further analyses as parentage analysis showed an improvement in assignment success without it. We therefore conducted the following analyses with a total of eight loci.

With GenAlEx 6.41(Peakall & Smouse, 2006) we performed a spatial structure analysis to analyse the change of pairwise genetic distance with increasing geographical distance in the different sexes. Short dispersal distances result in a positive genetic structure, with genetic similarity inversely correlated with spatial distance between individuals (Wright, 1943). Spatial autocorrelation uses genetic and pairwise distance matrices to calculate a spatial autocorrelation coefficient (r). The autocorrelation coefficient provides a measure of genetic similarity between pairs of individuals within one spatial distance class using random permutation (9999 permutations in our analysis). It ranges from -1 to +1, with a mean of zero, which indicates no autocorrelation (Smouse & Peakall, 1999). Random permutations provide a 95% confidence interval around the null hypothesis of no spatial autocorrelation and a significant positive or negative genetic structure is reached when r falls outside this confidence interval. Eight distance classes of 1000 m each were chosen based on home range calculations of 26 slender mongooses (Graw & Manser, 2015b) and the maximum distance between pairs of animals in our study population. Because it was not possible to calculate home ranges and therefore home range centres for all individuals, we based geographical location of individuals on capture locations; mean locations were calculated when the same animal was captured several times. Only animals that were alive at the same time were included in the spatial autocorrelation analysis (23 males, 33 females).

In a second analysis we conducted a Mantel test (Mantel, 1967) that evaluated correlations between two distance matrices. Here we looked at the change of pairwise relatedness with changing social distance between animals of the same sex, using 9999 permutations. Pairwise relatedness coefficients (Queller & Goodnight, 1989) were calculated in GenAlEx. Social distance was defined in three categories: belonging to the same spatial group; being in neighbouring spatial groups; and pairs in nonadjacent spatial groups. Mantel tests calculate a correlation coefficient (Mantel statistic R_{xy}) ranging from -1 to 1, indicating the strength of the relationship (0 = no relationship, 1 = strong positive, -1 = strong negative relationship). The

associated *P* value represents the proportion of simulations for which the associated correlation coefficient was greater than or equal to the observed Mantel statistic. We used a partial Mantel test (Anderson & Legendre, 1999) to test between subsets of social distance classes (same versus neighbouring spatial group, neighbouring versus nonadjacent spatial group, same versus nonadjacent spatial group). Partial Mantel tests evaluate the correlation between two distance matrices while controlling for the effect of a third. In our case the third matrix was binomial, defining which pairs of mongooses to include.

In addition to the spatial-autocorrelation methods described above, we tested for sex-biased dispersal with FSTAT 2.9.3.2. (Goudet, 2002), using F_{ST} values (the total genetic variance among groups) and the mean corrected assignment index (mAIc) for adult (postdispersal) male and female slender mongooses using local spatial group as substructure. Since allelic frequencies among groups should be more similar in the dispersing sex, F_{ST} should be higher for the philopatric sex. Corrected assignment values of individuals determine the probability that an individual genotype appears in the population from which it was sampled, correcting for differences in population genetic diversity (Farve et al., 1997). A positive AIc value indicates a more than average likelihood that this genotype will occur in its sample and is therefore probably a resident, while a negative AIc indicates a less likely than average genotype and probably a disperser (Goudet, Perrin, & Waser, 2002). We used F_{ST} and mAIc because in simulations with varying sampling size and regime as well as dispersal bias, these proved to be the most powerful parameters (Goudet et al., 2002). We conducted a two-tailed test with 10 000 randomizations.

Furthermore, we conducted a parentage analysis of adult slender mongooses in COLONY 2.0.1.3 (Wang, 2004, Wang & Santure, 2009), which allowed us to compare the spatial locations of adults with that of their assigned parents. COLONY allows the inclusion of known parents, as well as exclusion of animals that are known not to be the parents. We only

considered mongooses as potential parents of other adult mongooses if this matched our age estimations. To be assigned as parents, candidates had to have one or no mismatches with their potential offspring and a probability of more than 90% of being the parent. We used the following parameters to run COLONY: mating system: polygamy for males and females; medium likelihood precision; probability a parent is included in the candidates: males: 0.65; females: 0.75. All other parameters were left at the default settings. Error rates and allele frequency were provided (see below).

<H1>Results

<H2>Observational and tracking data

<H3>Females

Between July 2008 and January 2011 a total of 42 adult female slender mongooses were caught. We documented four (9%) dispersal events based on recapture data. Three of these females were first caught as young subadults in their natal range. The fourth female was born during the study period. Dispersal distances for these females ranged between 0.9 and 3.1 km (average: 1.9 km; based on capture sites). Three females settled in the range of a neighbouring spatial group, while the fourth moved across the range of the neighbouring group to settle in the next. Two females were later found to be breeding (lactating) in their new home range; for the other two no data were available. Of 17 female pups that were born and could have reached adult status during the study period, none was caught again in its natal range past the age of 10 months.

291 <H3>Males

292 Based on capture and tracking data on a total of 33 adult males, we have anecdotal evidence
293 of dispersal in two adult males. Both were caught as fully grown adults, weighing over 600 g
294 and radiocollared because we initially thought them to be territorial males. During the
295 consecutive tracking events it became apparent that they were moving further and further
296 away from our study site. In both cases the collar was removed before we lost them
297 completely. One of them had at this point moved 4.5 km from his original capture location
298 (distance between capture location and last track); the other moved 2.9 km before we removed
299 his collar. In comparison, distances between capture sites for philopatric males were 35–960
300 m. We only identified one male pup that was born in our study groups and reached adulthood
301 during the study period. This male stayed in his natal range after the death of his mother to
302 become a breeding male. Three more male pups did not reach adult status before captures
303 ceased. They were last seen as subadults in their natal ranges, allowing no conclusion in terms
304 of their dispersal status.
305

306 *<H2>Spatial structure analysis*

307 Autocorrelation between genetic and geographical distance revealed a difference between
308 males and females in their dispersal pattern. Spatial structure analysis showed a significant
309 positive autocorrelation between genetic and geographical distance within the first spatial
310 distance class (0–1000 m) for male slender mongooses (N=16, r=0.116, P=0.002; Fig. 1a.).
311 Autocorrelation dropped below the 95% CI within all other spatial classes. This indicates that
312 males living within 1000 m of each other were on average more closely related than males
313 living further apart. Testing the overall significance of the correlogram (N=23) also yielded
314 significant results (omega value = 40.642, P= 0.002). Females (N=33) showed no spatial
315 autocorrelation until 7000 m. At this distance females seemed to be on average more closely

316 related to each other than across other distances (N=16, r=0.066, P=0.021; Fig. 1b.). The
317 overall correlogram of females was not significant (omega value = 23.418, P= 0.125).

318

319 Correlations between genetic relatedness and social distance class, i.e. the overlap in spatial
320 range, were found in males, but not in females. Mantel tests showed a highly significant,
321 negative correlation of pairwise genetic relatedness with social distance class in male
322 mongooses. The greater the social distance, the lower the relatedness between pairs of males
323 (R_{xy}=-0.386, P<0.001; Fig. 2a.). Males within the same spatial group were on average more
324 closely related than males in neighbouring and nonadjacent groups. Partial Mantel tests
325 revealed all correlations between subsets of social distance classes to be significant.
326 Differences in relatedness were stronger between males of the same and neighbouring spatial
327 groups (R_{xy} =-0.522, P<0.001), as well as of the same and nonadjacent spatial groups (R_{xy} =-
328 0.522, P<0.001), than between neighbouring and nonadjacent spatial groups (R_{xy} =-0.143,
329 P=0.029). For females no differences in pairwise relatedness based on social distance was
330 found (R_{xy} =-0.015, P<0.329; Fig. 2b.).

331

332 *<H2>Test for sex-biased dispersal*

333 Testing 64 adult slender mongooses, belonging to eight different spatial groups, for sex-
334 biased dispersal, revealed that the F_{ST} value for males (0.0969, N=26) was significantly higher
335 than for females (0.0049, N=38, P=0.004), indicating female-biased dispersal. The mAIc for
336 males was 1.3734 and for females -0.9397 (P=0.001), showing females to be immigrants
337 more often.

338 *<H2>Evidence for dispersal based on parentage analysis*

339 <H3>Females

340 Of 42 adult females included in our parentage analysis, we were able to identify the mother or
341 both parents for eight (19%) of them (two both parents, six only the mother). All of these
342 females were found to be dispersers (Table 1). In four cases, dispersal status could not be
343 detected, because the mother was unknown and we could not exclude that the identified father
344 had mated with a female outside his home range. The average dispersal distance for females
345 at the study site based on parentage analysis results was 3.43 km (range 1.6–6.8 km). Five of
346 the females moved through one to two spatial group ranges before settling in their new home
347 range. Three moved into the neighbouring spatial group's range and one female remained in
348 her paternal spatial group but moved across two female ranges before settling (see Fig. 3).
349 This last female moved 2.1 km from one end of her natal group's range to the other and did
350 not breed with any of the sampled resident males. Three females were found to be breeding in
351 their new range.

352

353 <H3>Males

354 Of 32 adult males included in our parentage analysis, we were able to determine the mother or
355 both parents for 15 (45%, five both, 10 only the mother). We found evidence for male
356 philopatry in 14 of these 15 males (93%; Table 1). One male (7%) showed possible dispersal,
357 having moved 2.3 km from his known mother's range. Of the five males that had both parents
358 determined, three remained in both their mother's and father's range, and the remaining two
359 stayed in their mother's spatial group but the father was a neighbouring male with whom they
360 did not seem to overlap. Out of three cases in which only the father could be determined, two
361 males remained in their father's range and one was a possible disperser moving 2.7 km away
362 from the range his father occupied. Firm conclusions are difficult as the possible disperser

363 was caught in the neighbouring spatial group's range, leaving open the possibility that this
364 was a philopatric male, whose mother had mated with a male outside her spatial group. Four
365 of the philopatric males were found to be breeding in their natal territory, although not with
366 their mothers.

367

368

369 **<H1>Discussion**

370 Our results using capture–recapture methods and four different genetic tests for dispersal in
371 the Kalahari slender mongoose, although based on a small sample size, indicate a sex-biased
372 dispersal rarely seen in solitary mammal species. Females are the predominant dispersers
373 while males are the more philopatric sex. Males living in the same spatial group were more
374 closely related than they were to neighbouring males or to those in nonadjacent territories.
375 Females, on the other hand, were as unrelated to females in their own spatial group as to
376 females outside their group. Of adult males with the mother or both parents identified, 93%
377 were philopatric, while none of the females in the parentage analysis remained in their natal
378 range. Of 17 female pups born during our study, none was seen in her natal range past the age
379 of 10 months, whereas of the four male pups born at least one remained in his natal range to
380 become a breeding male. There was anecdotal evidence for occasional adult male dispersal,
381 based on tracking data of two adult males that moved from their original capture locations
382 beyond the range of our study area. This could indicate that males do disperse less often and
383 possibly later but further than females, leaving the local population in search of unoccupied
384 ranges.

385 How can this unusual pattern of sex-biased dispersal in the Kalahari population of slender
386 mongooses be explained? It is likely that social systems and social interactions play a crucial

387 role (Lawson Handley & Perrin, 2007). Slender mongooses are solitary foragers living in
388 spatial groups with extensive male–male and male–female overlap, while female ranges are
389 more exclusive. Within spatial groups, communal denning can be observed, especially during
390 winter months (possibly for thermoregulatory reasons; Graw & Manser, 2015b). Groups of up
391 to five mongooses share a tree hole, in which males share with other males of their spatial
392 group and females, while females only share with adult males of their spatial group or their
393 offspring (Graw & Manser, 2015b). Avoidance of overlap and no indication of positive social
394 interactions with other females could indicate higher costs of resource competition for
395 females, making intolerance of other females and an exclusive range necessary to meet
396 energetic requirements (see Sandell, 1989). High resource competition is a driving factor of
397 dispersal (Greenwood, 1980; Lawson Handley & Perrin, 2007). Males, on the other hand,
398 might benefit from philopatry through kin cooperation in female defence (see Lawson
399 Handley & Perrin, 2007). Even though we did not detect any differences in home range size
400 for males living in the presence or absence of kin, there is some evidence for an increase in
401 reproductive success for kin-associated males (Graw & Manser, 2015b). Males in associations
402 overlap on average with more females (2.75 versus 1.75), seem better able to avoid
403 extragroup paternities (15% versus 21%), and sire on average more pups than nonassociated
404 males (average: 5.75 pups/male associated; 2.25 pup/male nonassociated, Graw & Manser,
405 2015b). Benefits through cooperation of related and unrelated males have been found in lions,
406 *Panthera leo*, and cheetahs, *Acinonyx jubatus*, in which males form coalitions. Cheetah males
407 in coalitions are better than single males in defending and holding an exclusive range
408 frequented by females (Caro, 1994). Male lions form coalitions that have greater success in
409 taking over a pride of females and holding it than solitary males (Packer & Pusey, 1982).

410 Females might also avoid costs of inbreeding depression by dispersing away from their
411 father's range. In species in which male tenure exceeds female age at first reproduction,
412 female offspring can avoid inbreeding with their father by dispersing away from their natal

range (Clutton-Brock, 1989; Clutton-Brock & Lukas, 2012). In slender mongooses age at first reproduction has not been resolved but is estimated to be around 2 years of age based on our recapture data. The longest recorded male tenure at our study site was 4 years by the time observations ended. Therefore male tenure seems to exceed female reproductive age in the slender mongoose and females could benefit from dispersal as a way of inbreeding avoidance, to avoid potentially mating with their fathers or close relatives. Unless alternative ways of kin recognition are used (such as major histocompatibility complex described for house mice, *Mus musculus*, Manning, Wakeland, & Potts, 1992), slender mongooses have no way of knowing who their father is by means of familiarity. Males, on the other hand, will be able to recognize their mother and avoid mating with her, while still gaining access to other unrelated females in their natal range. Although our sample size of male dispersers was small, they seemed to go much beyond the range of female dispersal, leaving, to the best of our knowledge, the local population. Neither recapture nor genetic data revealed any immigration of local males into our study groups. Reasons for dispersal on this larger scale are most likely to be different from those for local dispersal; instead of being driven by kin competition and inbreeding avoidance, such dispersal seems necessary to escape crowded conditions and to find and colonize vacant territories (Fontanillas, 2004). Further investigation of dispersal distances of males and the territories from which they came (number of males already present, number of available females) are necessary to make firm conclusions.

Our findings are contrary to the results of the only other long-term field study on slender mongooses in the Serengeti (Rood & Waser, 1978). However, conclusions as to why there seem to be differences in dispersal behaviour between the two subpopulations are difficult due to the limited data available from the Serengeti, which appears to be based on mostly one spatial group. Here, all male slender mongooses disperse over great distances and no evidence for male philopatry was found (Rood & Waser, 1978, Waser et al., 1994). Females in the Serengeti normally disperse over short distances and settle close to their natal range, and they

439 can also occasionally remain in their mother's range past maturity and inherit the maternal
440 range (Waser et al., 1994), which we never observed in the Kalahari. In both populations
441 males formed associations, but while Kalahari associations consisted exclusively of related
442 males in their natal range, Serengeti formations could consist of related and unrelated males
443 that dispersed together or met after dispersal (Waser et al., 1994). There seem to be large
444 differences in population density between the sites. In the Kalahari we estimated the
445 population density to be around 1.6–2.0 adult slender mongooses/km^2 (unpublished data),
446 while in the Serengeti it was estimated at 5.3 slender mongooses/km^2 (Waser, Elliott, & Creel,
447 1995). Similarly, slender mongoose ranges differed significantly between the two study sites.
448 In the Kalahari, ranges are much bigger with 1.83 km^2 for males and 1.06 km^2 for females
449 (Graw & Manser, 2015b), compared to 0.7–0.8 km^2 for males and 0.3–0.5 km^2 for females in
450 the Serengeti (Rood, 1989). It is possible that it might be necessary for all Serengeti males to
451 disperse to escape already saturated ranges with high local mate competition, while in the
452 Kalahari it can pay for males to stay in their natal range to help control the big range and the
453 females within more effectively against outsiders. The differences could possibly indicate
454 flexibility in dispersal behaviour within the species to ecological factors such as range
455 saturation and mate availability, resulting in male dispersal in the case of overcrowding and
456 high mate competition. Also, males in the Kalahari might occasionally be forced to disperse
457 when their natal range is already saturated with males (see above).

458 A female-biased dispersal system is uncommon among mammals but even more so among
459 solitary mammals, in which typically both sexes disperse. The pattern in slender mongooses is
460 similar to that in the other two solitary species with female-biased dispersal, the common
461 wombat and kinkajou. In the common wombat, males possibly cooperate with kin to defend
462 burrows, which are an important resource (Banks et al., 2002). In the kinkajou, females
463 disperse and males form patrilineal associations defending areas with rich food sources
464 (fruiting trees) to maximize the number of females with which they overlap (Kays &

Gittleman, 2001). Females are tied to food resources and avoid contact with other individuals to avoid feeding competition (Kays & Gittleman, 2001). Females have smaller, more exclusive ranges than males and avoid contact with other adult females. We do not have any evidence for cooperative male defence of ecological resources in the slender mongoose; instead males seem to gain reproductive benefits through enhanced defence of females. Unfortunately no information on male tenure and female age at first reproduction in the kinkajou and wombat is available, so the influence of inbreeding avoidance on driving female-biased dispersal remains unclear. The observed bias in sex ratio among offspring in the slender mongoose is unlikely to be explained by a sampling error. However, whether and in what way such a bias in sex ratio has an influence on dispersal (Julliard, 2000) needs further investigation.

Data on dispersal in other mongoose species are limited to observations and tracking of marked animals, most commonly showing dispersal by both sexes, and dispersal seems closely linked to gaining mating opportunities. Males and females in meerkats, dwarf mongooses, *Helogale parvula*, banded mongooses, *Mungos mungo*, and yellow mongooses can benefit from dispersal through gaining access to unrelated breeding partners and increasing their reproductive chances (Balmforth, 2004; Cant, Otali, & Mwanguhya, 2001; Clutton-Brock et al., 1998b; Doolan & Macdonald, 1996; Rood, 1990; le Roux, 2007; Stephens, Russell, Young, Sutherland, & Clutton-Brock, 2005). They avoid mating competition with more dominant individuals in the group-living mongooses and all of them avoid inbreeding with related individuals (their parents and siblings) in their natal range or group. In the cooperatively breeding species (meerkats, dwarf mongooses, yellow mongooses in high-density populations), dispersal occurs when benefits gained by risking dispersal and potentially finding a mate and gaining breeding status outweigh benefits gained through indirect fitness when helping to raise related offspring (Doolan & Macdonald, 1996; Rood, 1990; Vidya, Balmforth, le Roux, & Cherry, 2009). In the communally breeding banded

491 mongoose, in which several females and males breed, individuals can be evicted as a result of
492 intense kin competition over breeding and breeding resources (helpers) or disperse potentially
493 to avoid inbreeding depression (Cant et al., 2001).

494 Slender mongooses are unique among these mongooses not only due to the intense sex bias in
495 dispersal but also because they are the most solitary. Unlike the more social species, reasons
496 for dispersal and philopatry seem to differ between the sexes in slender mongooses. In the
497 Kalahari, slender mongoose females predominantly disperse, probably to avoid inbreeding
498 and resource competition. Male slender mongooses are often able to breed in their natal range
499 without the danger of inbreeding or intense mate competition, while this does not seem to be
500 the case for males in the social species. If slender mongoose males disperse we assume this to
501 happen when ranges are overcrowded with males, resulting in a lack of access to females and
502 intense male mate competition. Similarly only male slender mongooses benefit from
503 philopatry (through kin cooperation in female defence), while in the other group-living and
504 cooperative mongoose species, including high-density yellow mongooses, both sexes equally
505 gain indirect reproductive benefits from remaining in their natal group and helping to raise
506 related pups (Balmforth, 2004; Clutton-Brock et al., 1998a; Doolan & Macdonald, 1996;
507 Gilchrist, 2004; Rood, 1990; Vidya et al., 2009). Unfortunately we lack data on dispersal
508 behaviour of other solitary mongoose species but the hypothesis of a species' social system
509 influencing its dispersal patterns (Lawson Handley & Perrin, 2007) seems to be supported by
510 these findings.

511 The Kalahari slender mongooses provide a rare case of female-biased dispersal and regular
512 male philopatry in a solitary mammal. Female slender mongooses in the Kalahari all disperse,
513 possibly to avoid inbreeding, while for males philopatry appears the most beneficial strategy.
514 We conclude that understanding the ultimate reason for sex-biased dispersal can be promoted
515 by looking at species that deviate from common dispersal patterns and by comparing these

516 with closely related species of varying social systems. Yet, the differences between the two
517 slender mongoose populations in the Kalahari and in Tanzania also suggest that ecological
518 constraints have a large influence on the flexibility of dispersal patterns.

519

520

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750

751 **Appendix:** Cross-species amplification

752 As no primers were available for slender mongooses we tested a total of 40 primer pairs that
753 had previously been cloned in closely related mongoose species and other carnivores: 14
754 cloned from banded mongooses (Waldick et al., 2003), nine from meerkats (Griffin et al.,
755 2001), eight from the small Indian mongoose, *Herpestes javanicus* (Thulin et al., 2002), four
756 from seals (*Arctocephalus gazella, Halichoerus grypus* and *Mirounga leonina*, Allen, Amos,
757 Pomeroy, & Twiss, 1995, Goodman, 1997), three from the domestic cat, *Felix catta* (Menotti-
758 Raymond & O`Brian, 1995), one from domestic dogs, *Canis familiaris* (Holmes et al., 1995)
759 and one from the Sumatran tiger, *Panthera tigris sumatrae* (Williamson, Huebinger, Sommer,

760 Louis, & Barber, 2002). For the loci Ssu13.8 and Mm18.1 we used modified versions of the
761 original primers (Nielsen et al., 2012; Young et al., 2007). In a first step we tested all primers
762 for amplification in the slender mongoose, using DNA from only one adult individual. A
763 touchdown polymerase chain reaction (PCR) protocol was employed to cover a wide array of
764 annealing temperatures and the Qiagen multiplex PCR Kit using 20–50 ng of DNA with 0.1–
765 0.4 µM of each primer. Each step consisted of 30 s denaturation at 94 °C, annealing for 45 s at
766 60, 57, 54 and 50 °C (eight cycles per annealing temperature) and an extension for 60 s at 72
767 °C. These touchdown steps were preceded by an activation step at 94 °C for 15 min and
768 followed by a final extension at 72 °C for 10 min. PCR products were visualized on a 48-
769 capillary ABI 3730 DNA-Analyzer (Applied Biosystems). Thirty-three loci showed
770 amplification and were further tested for polymorphisms with the same touchdown PCR
771 protocol and five to nine slender mongoose DNA samples. Of these, 11 microsatellite loci
772 were chosen to genotype individuals, based on how well they amplified and their number of
773 alleles. Ssu7.1, Ss10.1, Ssu13.8 and Ssu13.9 were first described in meerkats (Griffin et al.,
774 2001), Mm18.1 and Mm18.2 in banded mongooses (Waldick et al., 2003), Hj34, Hj45 and
775 Hj56 in the small Indian mongoose (Thulin et al., 2002), AHT130 in the domestic dog
776 (Holmes et al., 1995) and Ag6 in the Antarctic fur seal (Ag6, Hoffman et al., 2008). For the
777 loci Ssu13.8 and Mm18.1 we used modified versions of the original primers (Nielsen et al.,
778 2012; Young et al., 2007).

779

780

781 **Table 1:** Results of parentage analysis for adult slender mongooses with natal and current spatial group

782 membership and dispersal distance

	Analysed	Parents	%	ID	Mother	Father	Natal	Current	Dispersal distance	Comment
Females	43	13	30	SLF09	SAF07		A	L	6.8	
				SBF12	SDF06		D	B	5.2	
				SDF21	SRF03		R/B	D	3.6	
				SGF21	SGF08		B	G	3.2	
				SGF08	SGF02	SGM01	G	B	3.1	
				SDF06	SDF04		D	D	2.1	Across 2 female ranges
				SDF17	SMF09	SMM05	M	D	2.0	
				SMF23	SGF08		B	M	1.6	
				SPF02		SAM03	A?	P	?	
				SFF07		SFM02	F?	F	?	
				SDF18		SRM02	R?	D	?	
				SRF09		SRM01	R?	A	?	
Males	33	19	58	SGM06	SGF02	SGM01	G	G	0	
				SRM02	SRF03	SRM05	R/B	R/B	0	
				SAM06	SAF07	SAM03	A	A	0	
				SDM01	SDF04	SRM02	D	D	0	
				SCM04	SCF02	SRM01	C	C	0	Breeding
				SMM03	SMF04		M	M	0	Breeding
				SMM05	SMF04		M	M	0	Breeding
				SDM02	SDF04		D	D	0	
				SFM09	SFF07		F	F	0	
				SGM17	SGF10		G	G	0	
				STM01	SGF10		G	G/T	0	
				SRM01	SRF03		R/B	R/B	0	Breeding
				SBM08	SRF10		R/B	R/B	0	
				SRM12	SRF10		R/B	R/B	0	
				SAM03	SFF07		F	A	2.3	
				SAM02		SAM03	A?	A	0?	
				SDM16		SDM07	D?	D	0?	
				SDM22		SAM03	A?	D	2.7?	

783

Table A1: Microsatellite loci chosen to genotype slender mongooses

Primer	Sequence	Species isolated from	Range (bp)	Alleles	H_O	H_E	*P*	Source
Mm18.1	GTTTGATTATATTGTATACCTGAAGCAC CTATTTTCTCAGTATAGCAGAAGGTG	Banded mongoose	147-163	9	0.738	0.832	0.0535	Nielsen et al., 2012
Mm18.2	TTGTTGCTGATTGTCTTC CAAGGTTCAGAAACTATGGA	Banded mongoose	196-230	11	0.787	0.861	0.2113	Waldick, Johnson, & Pemberton, 2003
Ssu13.8G	GATCAGTGAGAACAGAAGTGC ACCTCCTCCTCCAGATGCATC	Meerkat	192-210	10	0.877	0.845	0.4696	Young, Spong, & Clutton-Brock, 2007
Ssu13.9*	AACACACTTGAGGAATCTGACTC TTGGATGCTTAACCGAGCTAC	Meerkat	242-272	15	0.814	0.904	0.0588	Griffin, Nürnberger, & Pemberton, 2001
Ssu7.1	ATCCCTTAATGCATAGGCACAC CTGCTACTGTTTTCAAATATGC	Meerkat	163-193	12	0.918	0.892	0.2624	Griffin et al., 2001
Ag6	CCTGAGGCTCCTTCTTTCCT CCAGGACCAGTGGGAAGTTA	Antarctic fur seal	144-162	9	0.852	0.819	0.983	Hoffman, Dasmahapatra, &Nichols, 2008
Hj34†	TACAGGCAGTTAGAAGTCACATTT GAGTTCAAGCCCCACATCAGAG	Small Indian mongoose	175-199	8	0.77	0.74	0.0334	Thulin, 2002
Hj45	TCAATTTGCCGTCCTTTACA GGGCTTTTGGGTTACTTTTG	Small Indian mongoose	219-239	9	0.787	0.825	0.5892	Thulin, 2002
Hj56	AGCCCCAAATCAGACTC GAACTGGGCTGGAATCT	Small Indian mongoose	216-238	8	0.623	0.653	0.4954	Thulin, 2002
Ss10.1	GTGAGTAGATACTTTATCATCC ACCAGGAACATTGAAGCC	Meerkat	135-159	11	0.77	0.842	0.1916	Griffin et al. 2001

H_O=observed heterozygosity, H_E=expected heterozygosity, *P*= level of significance at which a locus deviates from HW equilibrium.

*Excluded due to the presence of null alleles.

†Excluded due to HW inequilibrium.

794

795 **Figure 1**: Change in genetic distance with spatial distance for (a) males and (b) females; red
796 dotted lines indicate the 95% confidence interval with upper and lower bounds, the blue line
797 charts average *r* across spatial distance classes

798

799 **Figure 2**: Change in pairwise relatedness with social distance (same spatial group,
800 neighbouring groups, nonadjacent groups) for (a) males and (b) females.

801

802 **Figure 3:** Map of the study site showing the results of the parentage analysis. (a) Dispersal of
803 eight females indicated by place of birth, capture sites after dispersal and dispersal direction.
804 Where the mothers were radiotracked, a rough depiction of the range, typical for adult
805 females, is given for size reference. (b) Capture sites for male offspring, mothers and where
806 available fathers indicate philopatry for nine of 10 males. Range estimations are given for
807 radiocollared mothers. As the data are based on adult individuals from our parentage analysis,
808 it was, in most cases, not possible to give exact birth locations; therefore capture sites/ranges
809 of identified mothers were used to estimate these.

810